TAXONOMY AND POSTMARSUPIAL DEVELOPMENT OF A DOMINANT DEEP-SEA EURYCOPID ISOPOD (CRUSTACEA)

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Abstract.—*Eurycope iphthima* n. sp. is a valuable subject for studies of systematics and population biology in abyssal Crustacea because of it numerical dominance, size, and robustness. In this introductory paper, the species is described, and developmental variation is discussed for the following characters: pereopod VII, antennula, rostrum, uropods, oostegites, and male pleopods I and II. Some evidence indicates this species is facultatively hermaphroditic and its sexual development is partly independent of somatic growth.

Because deep-sea sampling is so difficult, the biology of few abyssal benthic Crustacea is known well enough to examine problems of ontogenetic and population variation. Yet a knowledge of variability is critical to a clear understanding of the systematics of a group. In order to make these types of analyses in an important deep-sea group, the Eurycopidae, this paper introduces *Eurycope iphthima* new species, a dominant abyssal isopod. This species has a large body allowing its retention by standard sampling techniques: the smallest post-marsupial individuals are greater than one millimeter in length. Of additional value, *E. iphthima* has a very robust body, insuring undistorted specimens that are relatively easy to measure. Furthermore, *E. iphthima* has potential ecological importance to deep-sea faunal assemblages because of its numerical dominance in some areas. In two large epibenthic sled samples collected during Woods Hole Oceanographic Institution (WHOI) cruise no. 106 (stations 326 and 328), this species is the most abundant isopod, accounting for 23% of the total individuals. This introductory paper describes *Eurycope iphthima* n. sp. and the post-marsupial development of a number of its systematically important characters. Subsequent papers will discuss the taxonomy, population biology, and zoogeography of this important species.

Terminology.—Hessler (1970) reviewed the terminology used for the development of asellote isopods and concluded that the most informative system is that of Zimmer (1926), introduced for cumacean development. In this paper, the updated system of Hessler (1970) is used, except that the juvenile stage is not directly associated with instars due to this species' complicated development (discussed below). Because three preparatory female stages

before the brooding stage are recognized (Fig. 9D–F), the number after preparatory refers to the developmental stage, rather than the number of times the animal has entered that condition (as in Hessler, 1970), e.g., preparatory 3 female means the third and final preparatory female intermolt stage.

For structures on pleopods I and II of the male, the reader is referred to the excellent paper by Veuille (1978a), whose descriptive terms are used here with the exception that instead of his term, copulatory whip, stylet is used (Fig. 10K) as in past papers (Hessler, 1970). The small, thin distal projection on the protopod of the male pleopod II (Fig. 10K) is called the vermiform appendage after Menzies (1962).

Measurements.—Measurements are made as described in Wilson and Hessler (1980), with the following additions. Overhang is the ratio between the length of the rostral projection from the frons (Fig. 8D—a), and the rostral length (Fig. 8D—b). The length of the medial lobe of the antennular article one (Fig. 7C—ml) is measured from the insertion of article two to the lobe's distal tip. In the male pleopod I length–width ratio, the width is measured at the proximal edge of the dorsal orifice (Fig. 10K—do).

Family Eurycopidae
Subfamily Eurycopinae
Eurycope iphthima, new species
Figs. 1–5

Holotype.—Preparatory 3 female, 7.0 mm long, deposited in the United States National Museum (USNM), catalog number 181106.

Paratypes.—10 individuals, USNM 181107; 5 individuals, American Museum of Natural History, New York, catalog number 16253; 5 individuals, Zoological Museum of the University of Copenhagen; 273 individuals retained in the collection of Robert R. Hessler, Scripps Institution of Oceanography.

Type-locality.—WHOI station 326, R/V *Chain* cruise no. 106, 22 August 1973, 50°04.9–05.3′N, 14°23.8–24.8′W, 3859 meters, estimated bottom temperature (from Fuglister, 1960) 2.5°C.

Derivation of name.—*iphthima* is Greek, meaning strong or stalwart, referring to the robust nature of the species.

Other material.—See Table 1.

General distribution.—Abyssal Central North Atlantic and the rise and slopes of Northeastern Atlantic, 2379–5000 meters.

Diagnosis.—Body length approximately 2.1 times width, cephalon widest at level of pereopod I coxae. Rostrum (Fig. 8) almost always with some overhang, especially when rostrum narrow, width varies around 0.1 cephalon width, with u- or v-shaped anterior notch. Female and immature an-
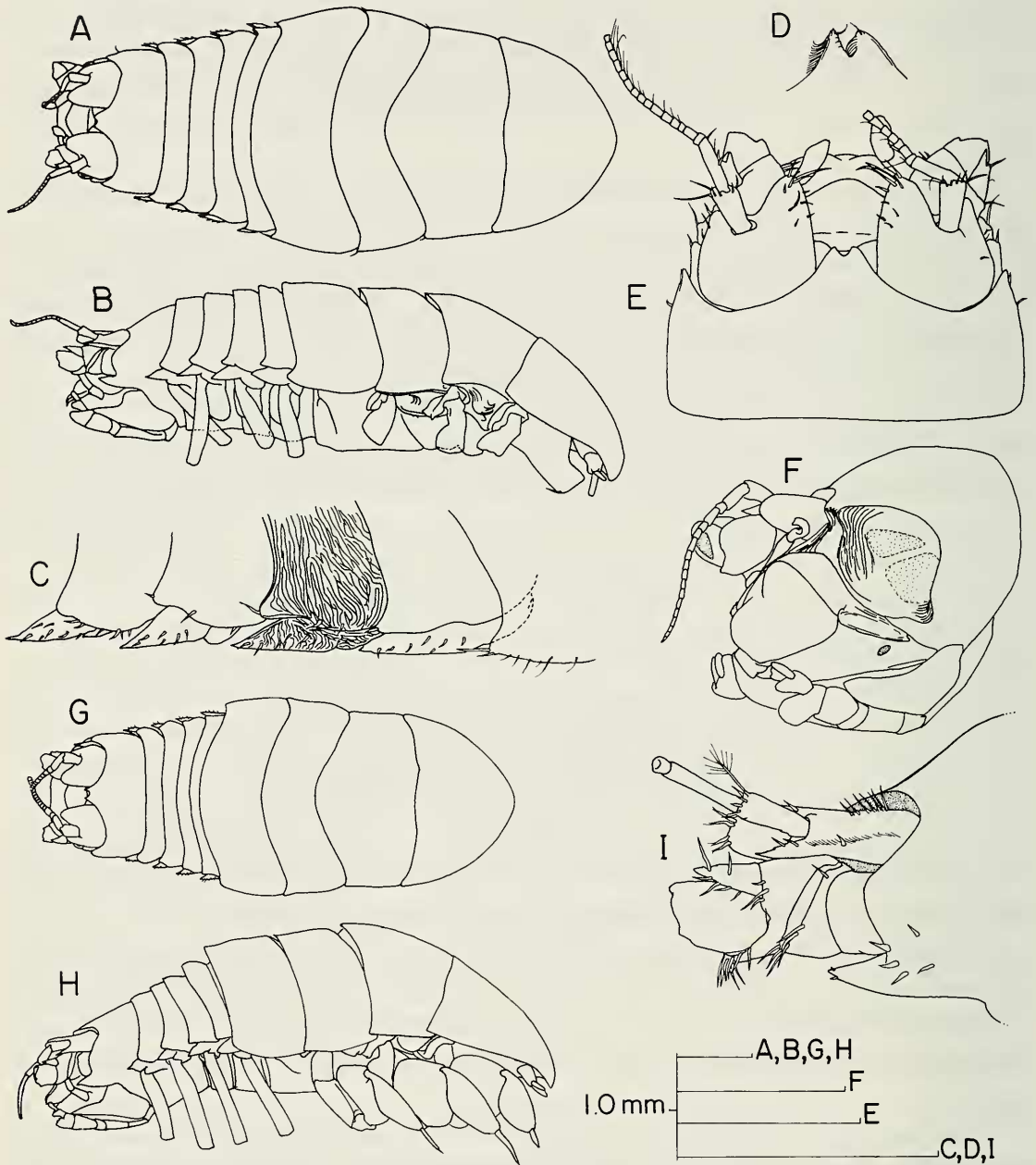
Fig. 1. *Eurycope iphthima*: A–E, I: holotype preparatory 3 female. A, Body, dorsal view; B, Body, lateral view; C, pereonites 1–4 and associated coxae, cuticular ridges shown only on pereonite 3; D, rostrum, left oblique view; E, Cephalon, dorsal view; F, Preparatory 2 female, cephalon, oblique frontal view, antennula and antenna removed on left side; G–H, Precopulatory adult male dorsal and lateral views; I, Cephalon, lateral view.

tennular third article (Fig. 7B) approximately same length as second article; basal article medial lobe slightly shorter than article 2; copulatory male antennular third article (Fig. 7B) slightly shorter than second article, basal article medial lobe around same length as second article, flagellar articles

Table 1.—Localities for *Eurycope iphthima* n. sp.

Station	Mean west latitude	Mean north longitude	Depth in meters	Number of samples	Number of individuals
*WHOI 326 (type locality)	50°05′	14°24′	3859	1	294
*WHOI 80	34°49′	66°34′	4970	1	3
WHOI 83?	34°46′	66°30′	5000	1	1 juv.
WHOI 121?	35°49′	65°10′	4800	1	2 frags.
WHOI 287?	13°16′	54°52′	4957	1	9 frags.
WHOI 288	11°03′	55°04′	4423	1	11
WHOI 318	50°27′	13°20′	2506	1	105
WHOI 321	50°12′	13°36′	2879	1	150
WHOI 323	50°08′	13°52′	3347	1	86
WHOI 328	50°05′	15°45′	4431	1	261
WHOI 330	50°43′	17°52′	4632	1	35
WHOI 334	40°43′	46°14′	4400	1	200
*Allen 50	43°46′	3°38′	2379	1	19
†INCAL 1.8	55°01′	12°36′	2890	4	18
INCAL 2.1	50°15′	13°12′	2641	4	108
INCAL 2.2	48°19′	15°23′	4829	1	12
INCAL 2.3	47°30′	9°34′	4284	11	96
INCAL 2.4	46°00′	10°21′	4802	1	1

* More information on these stations in Wilson and Hessler (in press).
† Expedition Intercalibration, described in Sibuet (1979).

after article 8 wider than long. Pleopod I of copulatory male (Fig. 10I–K) length 3.6 width, dorsal orifice position 0.68 medial length; distal tip truncate in ventral view, tapered medially, lateral lobes thin to ventrally-curving spines closely adpressed to medial lobe; medial lobe thick, rounded medially, thinning laterally to dorsal shelf. Pleopod II of copulatory male (Fig. 10K) with long vermiform process, 0.15 total pleopod length. Uropodal endopod length less than protopod width, exopod length greater than half endopod length (Fig. 9A–C).

Additional description and variation.—Body robust, natasome broadly rounded in dorsal view, vaulted, muscular. Lengths of mature adults greater than 4 to 5 mm, largest individuals may exceed 7 mm; females larger than males, median lengths (ranges) 5.5 mm (4.1–7.4) vs. 4.9 mm (4.0–6.3); mean stage 4 length 2.2 mm, standard deviation 0.1, range 2.0–2.5.

Rostral variability common (Fig. 8): median rostral length-cephalic width ratio 0.19, range 0.18–0.22; medial rostral width-length ratio 0.36, range 0.22–0.64; median overhang 0.28, range 0.0–0.33; rostrum rarely juts abruptly from frons; when rostrum narrow, overhang more distinct; median values vary from population to population.
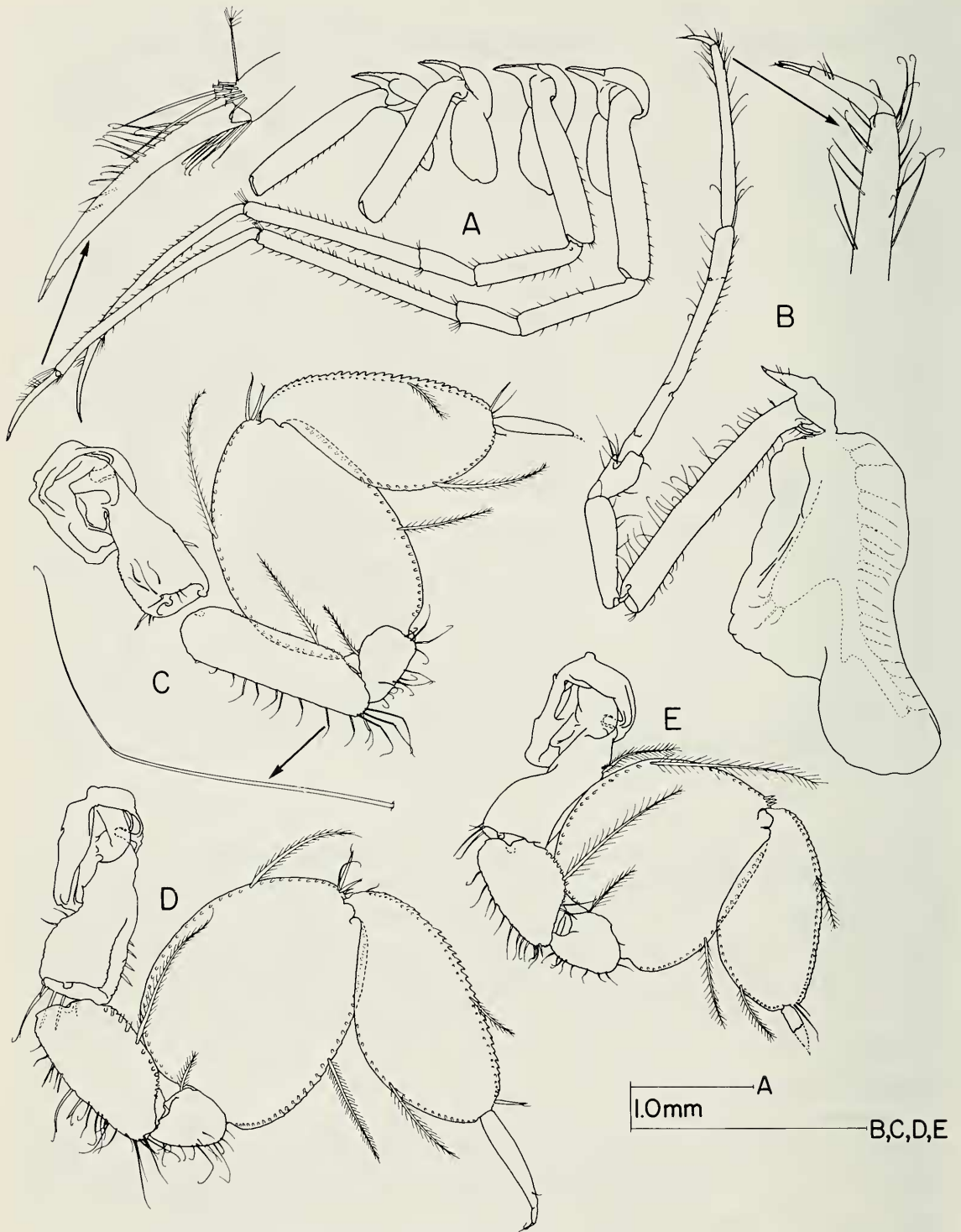
Fig. 2.   Pereopods: A, Pereopods I–IV, III–IV intact, dactylus IV enlarged; B, Pereopod I with oostegite, dactylus enlarged; C–E, Left natapods from precopulatory male: pereopod V, whip seta from ischium enlarged; pereopod VI; pereopod VII. Plumose setal rows indicated by basal insertions and single representative setae.
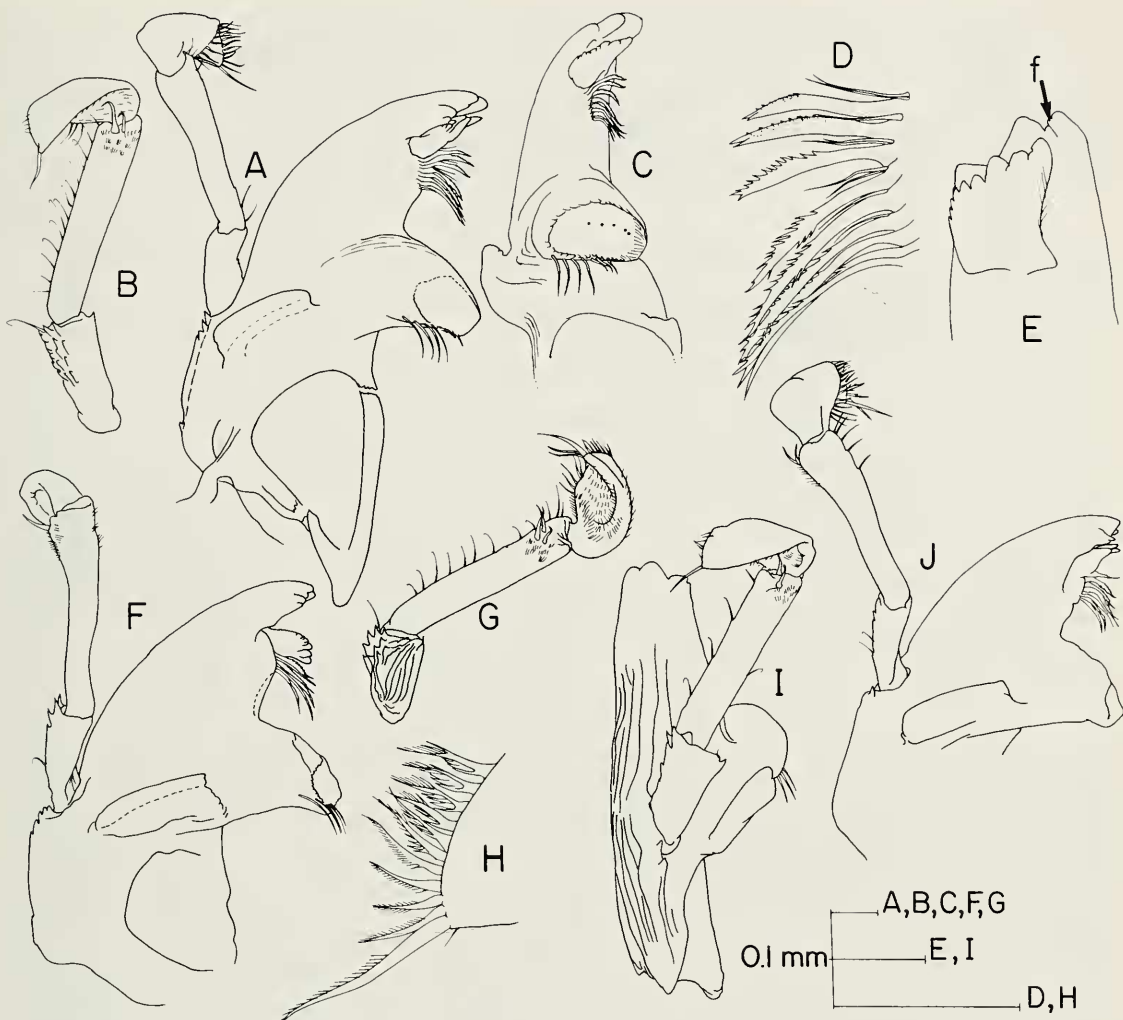
Fig. 3. Left mandibles: A–E, Preparatory 2 female. A, Dorsomedial view; B, Palp, lateral plan view; C, Medial view, plan view of triturative surface; D, Spine row, ventral view; E, Lacinia mobilis and incisor, posterior view, f—posterior fold in ventral tooth; F–H, Copulatory male. F, Dorsal view; G, Lateral view, palp in plan view; H, Setation of palp distal tip; I–J, stage 4 individual. I, Lateral view; J, Dorsal view.

Pereonite 7 medial length much greater than pereonite 5 or 6, pereonite 7 bulla enlarged and rounded; pereonites 5 and 7 subequal.

Antennula of copulatory male (Fig. 7D) with about 60 articles, length beyond proximal 2 articles 4.0 times length of article 1 medial margin; female antennula (Fig. 7B) values, 26 articles and 2.7 length ratio; basal article medial lobe with 5–7 unequally bifid setae in adults.

Left mandibular incisor (Fig. 3) with 3 large teeth, ventral tooth with fold in posterior surface (Fig. 3E—f), dorsal tooth with small tooth on dorsal side. Lacinia mobilis with 6 teeth on medial surface grading into 2–3 denticles on dorsal surface. Spine row with 7–9 spines having teeth or spinules
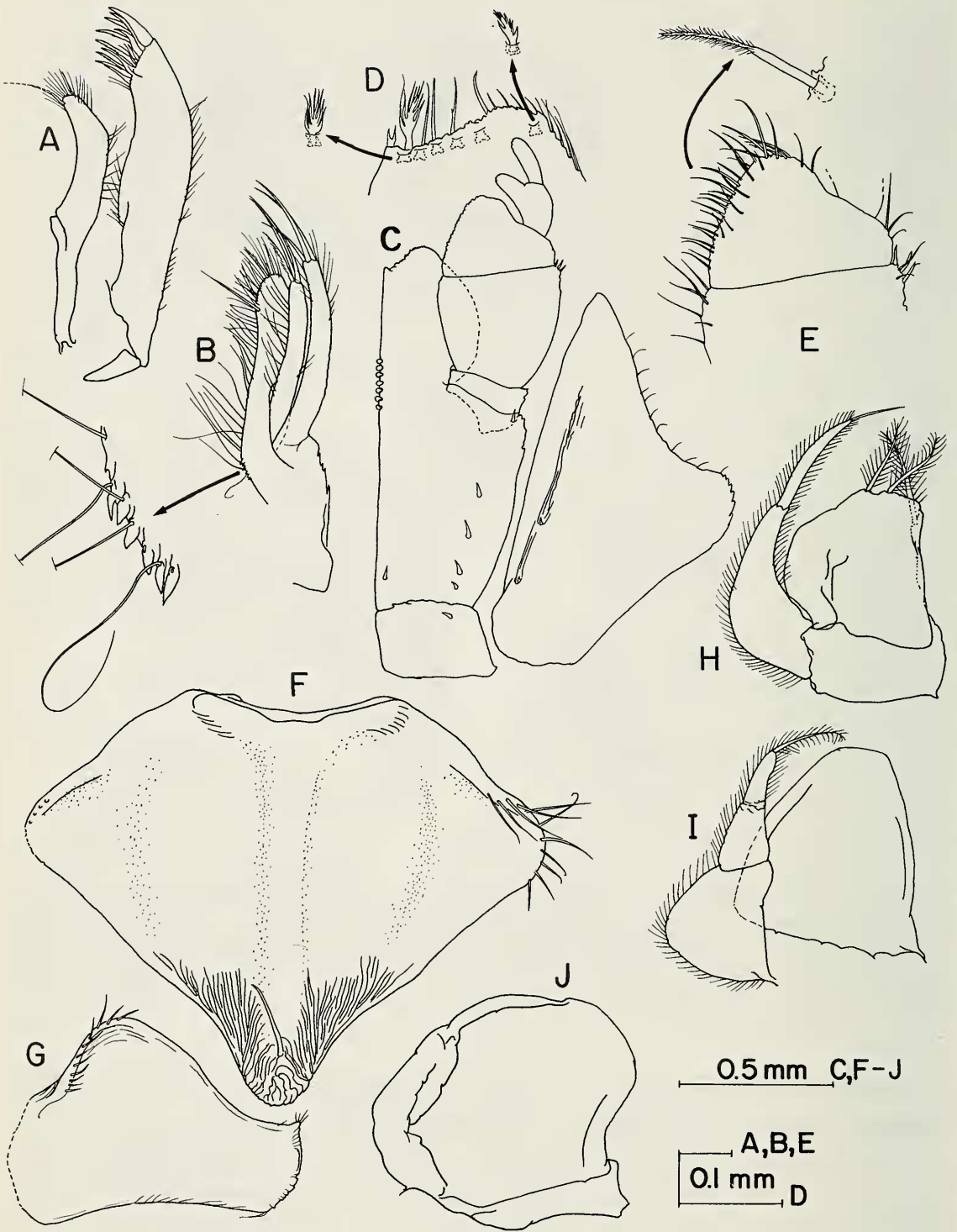
Fig. 4. Appendages from preparatory females: A, Maxillula; B, maxilla with enlargement of mediobasal denticles and setae; C–E, Maxilliped. C, Ventral view, epipod detached, setae not shown; D, Distal tip of endite, fan setae bases shown with examples to either side; E, Setation on palp articles 3 and 4; F, Pleopod II, ventral view, hemiplumose setae shown on left side, cuticular ridges shown only on apex and distal tip; G, Pleopod II, lateral view; H, Pleopod III; I, Pleopod IV; J, Pleopod V.

and very fine accessory setae on anteriormost 4–6 spines. Molar approximately same length as mandibular condyle; triturative surface oval, teeth on posterior and dorsal margins low and rounded, 6–8 setae on posterior margin. Mandibular palp shorter than mandibular body; male palp longer than female palp: male palp article 2 length 0.44 times mandible body length, female 0.38.

Maxilliped (Fig. 4C–E) in adults with 6–9 receptaculi, around 7 short thick unequally bifid setae on ventral face of coxa and basis; palp merus width 1.2 times endite width. Epipod broad with subquadrate lateral expansion, with 2–4 short thick setae on ventromedial ridge, length 1.8 times width.

Pereopod-body length ratios in pereopods I, III, IV: 0.74, 0.90, 1.05. Bases of pereopods I–II of copulatory male longer than in preparatory 3 female: copulatory male basis-body length ratios in first 4 pereopods 0.21, 0.20, 0.20, 0.22; for preparatory female 0.18, 0.19, 0.20, 0.20. Male pereopods (Fig. 2C–E) V–VII propodus width 0.51 times length, ventral setal row only on distal half of margin. Dactylus of pereopod VI largest of natatory limbs, pereopod VII dactylus smallest. Only one large seta at proximal posterior angle of pereopod VII basis.

Pleopod II of both sexes (Figs. 10K and 4F, G) with strongly recurved lateral margins. Male pleopods I (Fig. 10I–K) widest at insertion, with paired row of 9–10 hemiplumose setae. Male pleopod II (Fig. 10K) length 1.7 times width, depth 0.3 times length, with about 14 hemiplumose setae on each lateral margin. Stylet 0.69 times pleopod length. Female pleopod II (Fig. 4F–G) length 0.79 times width, depth 0.3 times length, with about 11 hemiplumose setae on lateral margins.

Uropodal protopod (Fig. 9A–C) strongly broadened medially, width greater than length, ventral and medial margins with dense row of long, thin unequally bifid setae.

Remarks.—*Eurycope iphthima* belongs to a speciose subgroup within the genus wherein the differences between the member species are small but definitive. Other described species in this subgroup are *E. complanata* Bonnier 1896, *E. hanseni* Ohlin 1901, *E. inermis* Hansen 1916, and *E. ratmanovi* Gurjanova 1946. These species are being revised and new species are being described in research now in progress.

Eurycope complanata is most similar to *E. iphthima* and occurs within the same geographic area although at much shallower depths. *E. complanata* is narrower in the body (l/w ratio 1.9) and has a narrower, less overhanging rostrum. Additionally, the antennular article 3 is distinctly longer than article 2 and the endopod of the uropod is longer than the width of the protopod.

Potential synonyms.—Menzies (1962, pp. 141–142) describes 4 individuals of *Eurycope complanata* collected by the R/V *Vema* in Lamont Geological Observatory Biotrawl no. 7 (5779 m 29°17.6′N, 57°20.3′W). The large male
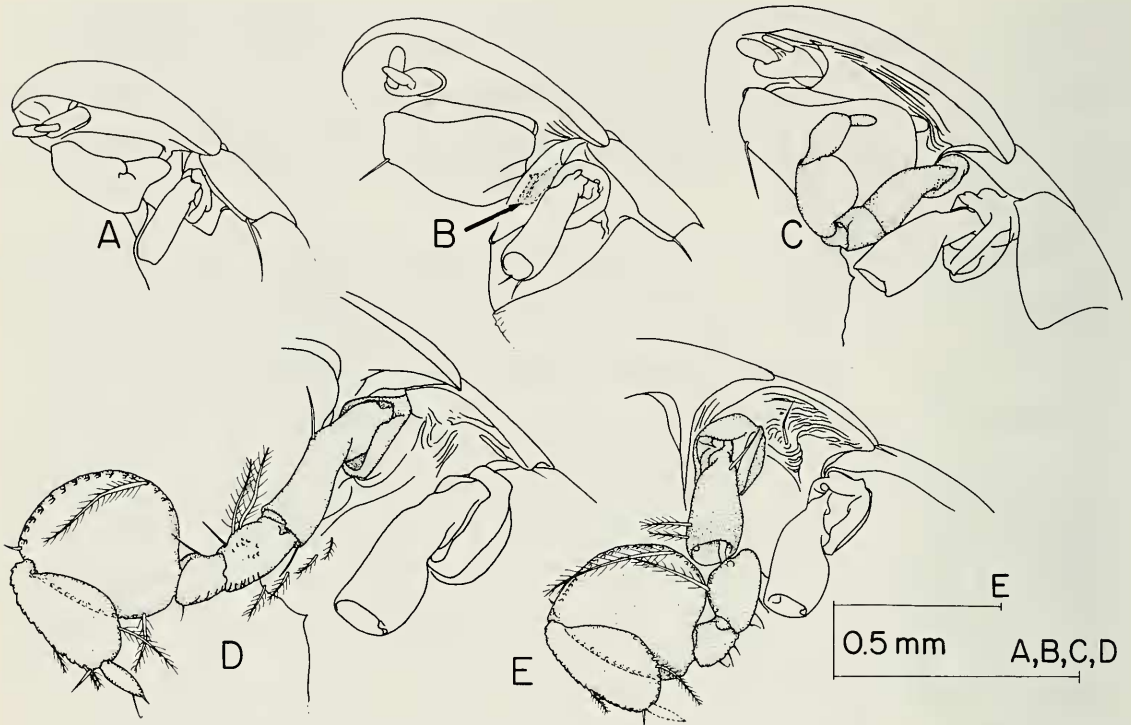
Fig. 5.   Development of pereopod VII: Pereopod VII shown darkened in right lateral oblique view; basis of pereopod VI included for comparison; only representative setae in plumose setal rows shown. A, Manca 1; B, Manca 2, arrow indicates pereopod anlagen below cuticle; C, Manca 3; D, Stage 4; E, Stage 6.

figured by Menzies appears to be *E. iphthima,* but this cannot be determined with certainty because this material seems to be missing from the collections of the American Museum of Natural History (H. S. Feinberg, pers. comm.). Chardy (1979) lists *E. complanata* as occurring at stations 2000 meters and deeper in the Bay of Biscay. The present data and other information show that *E. iphthima* occurs in the Bay of Biscay in this depth range and *E. complanata* occurs shallower, 860–1920 meters (Bonnier, 1896; Wolff, 1962; unpublished data).

Postmarsupial Development

The postmarsupial development of deep-sea asellote isopods has been reviewed by Wolff (1962) and Hessler (1970). More recently Thistle and Hessler (1977), and Haugsness and Hessler (1979) provide developmental data for 2 abundant eurycopids. This section will describe the development of several taxonomically important characters and discuss the relationship between somatic growth and sexual maturation in *Eurycope iphthima* and in the species studied by the above authors.

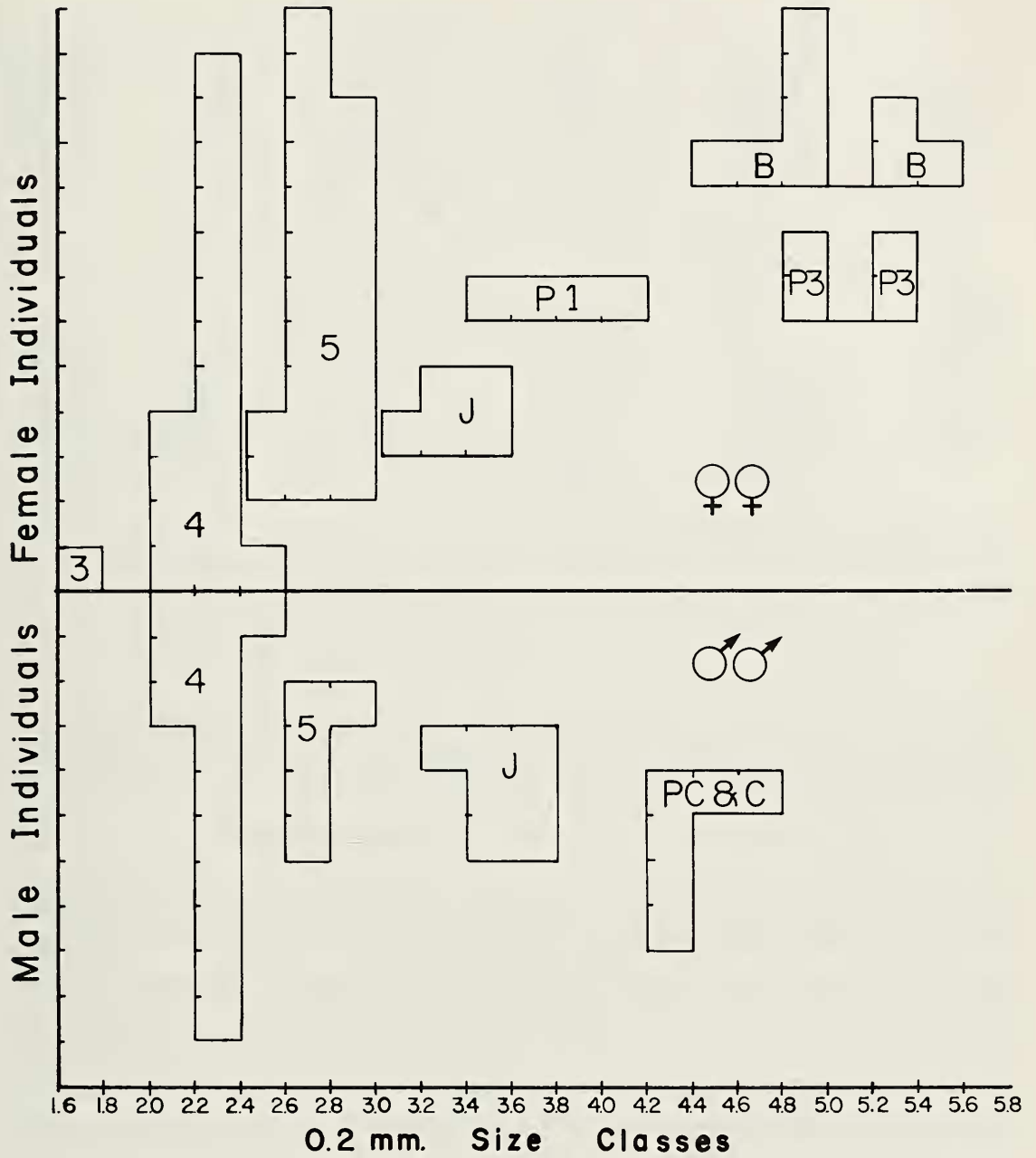*Pereopod VII.*—The first 5 stages can be recognized on the basis of the

Fig. 6. Representative body length-frequency histogram of all intact individuals from WHOI 318. Stages three to five, *3–5*. Juveniles, *J*. Precopulatory and copulatory, *PC&C*. Preparatory one, *P1*. Preparatory three, *P3*. Brooding, *B*. Individuals outside of the 1.7–5.7 mm range and preparatory two females appeared in other samples.

development of the seventh pereopod and pereonite (Fig. 5). Manca 1 has no apparent pereopod VII and the corresponding segment appears dorsally as a triangular plate having no lateral margins. The manca 2 pereopod is a subcuticular primordium and the pereonite is somewhat larger but still with no lateral margins. In manca 3 the pereopod is external but rudimentary
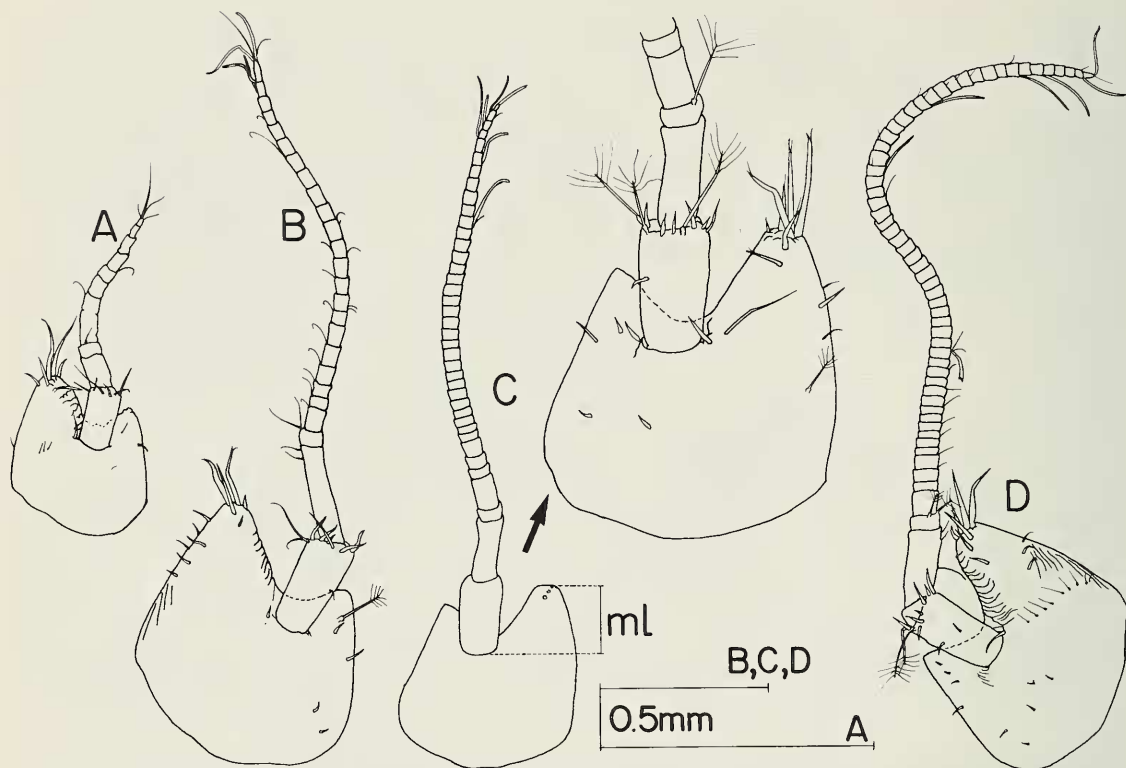
Fig. 7.   Development of the antennula: A, Stage 4 individual; B, Preparatory 2 female; C, Precopulatory male, enlargement showing setal detail, distance *ml* illustrates medial lobe length; D, Copulatory male, not all aesthetascs present.

with no functional joints or setae. At this stage the seventh pereonite becomes part of the lateral margin but the anterolateral corner is not pointed. Similar to *Jaera a. albifrons* Bocquet (1953) the stage 4 pereopod VII becomes functional but is distinctly smaller, with fewer setae compared to the anterior natapods. In most specimens where the distal parts of the limb have been lost in sampling, stage 4 can be recognized by a basis which is smaller and much less robust than the basis of pereopod VI. In stage 5 the basis is the same length as pereopod VI but slightly less robust. In stage 6 and larger, pereopods VII and VI bases are of approximately equal size and robustness.

Instar size.—Figure 6 shows a representative size-frequency histogram from WHOI 318 which illustrates most of the instars discussed below. *Eurycope iphthima* increases in length by roughly 1 mm in 2 molts. This increase is less for mancas (with these stages falling between 1 and 2 mm) and perhaps greater for older individuals. Mancas 1–3 were approximately 1.1, 1.4 and 1.8 mm respectively. Stage 4 averaged 2.2 mm, varying only one or two tenths in either direction. Significantly, the mean length for stage 4, which was well represented at the localities studied in detail, did not vary
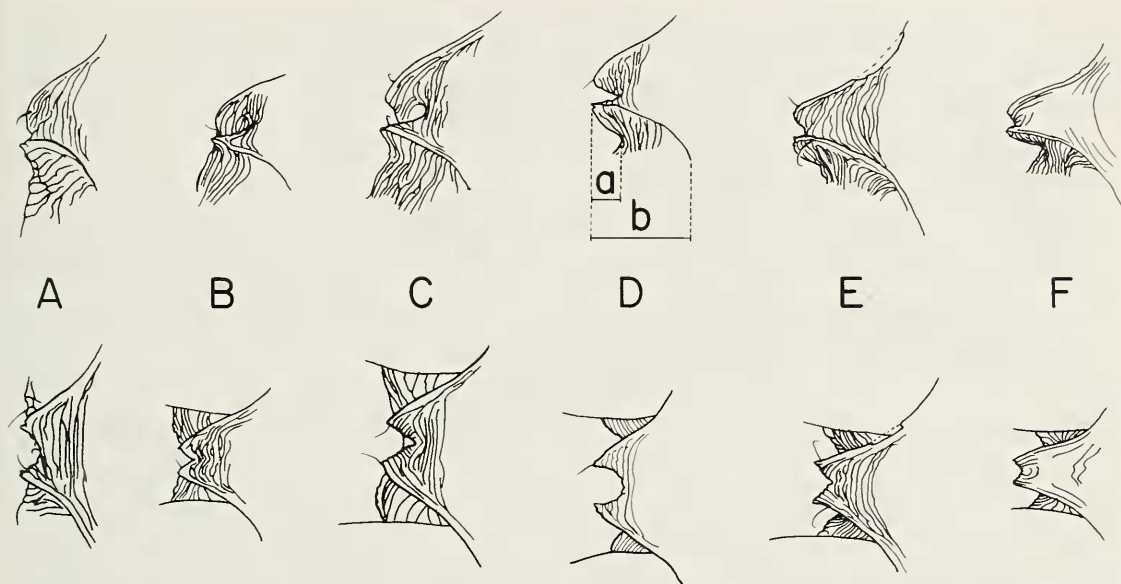
Fig. 8. Development and variation of the rostrum: Top illustrations, left oblique dorsal view; bottom illustrations, dorsal view; cuticular ridges shown. A, Stage 4 individual, 2.2 mm; B, Male, 5.1 mm; C, Preparatory 3 female, 6.7 mm; D, Preparatory 1 female, 5.8 mm, distance a is the rostral projection from the frons, distance b is the rostral length; E, Male, 6.5 mm; F, male, 5.1 mm. A–D, are common conditions; E–F are rare.

geographically. Stage 5 mean length at one abundant station (WHOI 318, Fig. 6) is 2.7 mm (SD = 0.14, N = 27, range = 2.4–2.9). Beyond stage 5 the molts are difficult to recognize, although at some localities they appear as modes in the size-frequency distribution. Sexual development cannot be used to recognize specific stages because it appears to be independent of size. Stage 6 is about 3.2–3.6 mm and stage 7 is at approximately 4.0–4.4 mm. Sexual maturity may occur at any stage after 7, the earliest being stage 8, roughly 4.4–5.0 mm. Beyond this stage the data do not allow a clear association between instar and size.

Antennula.—Besides the sexual pleopods, dimorphism is most apparent in the development of the antennula (Fig. 7). In mancas and stage 4, the flagellum has only a few articles, no aesthetascs and a more rounded medial lobe having 4 or 5 unequally bifid setae. One taxonomically diagnostic character, article 3 being subequal or shorter than article 2, is stable, even in these stages. As development proceeds, more articles are added to the flagellum with copulatory males achieving 50–60 articles and preparatory 3 females with only 20–25. Notably the females have aesthetascs only on the distal articles while in males they may occur on the full length of the flagellum. Male flagellar articles are wider than long and female articles are longer than wide. However, in spite of the shorter articles, the male antennula is longer. With increasing instar number the medial lobe becomes slightly more pointed and the distal setae increase to 6 or 7.
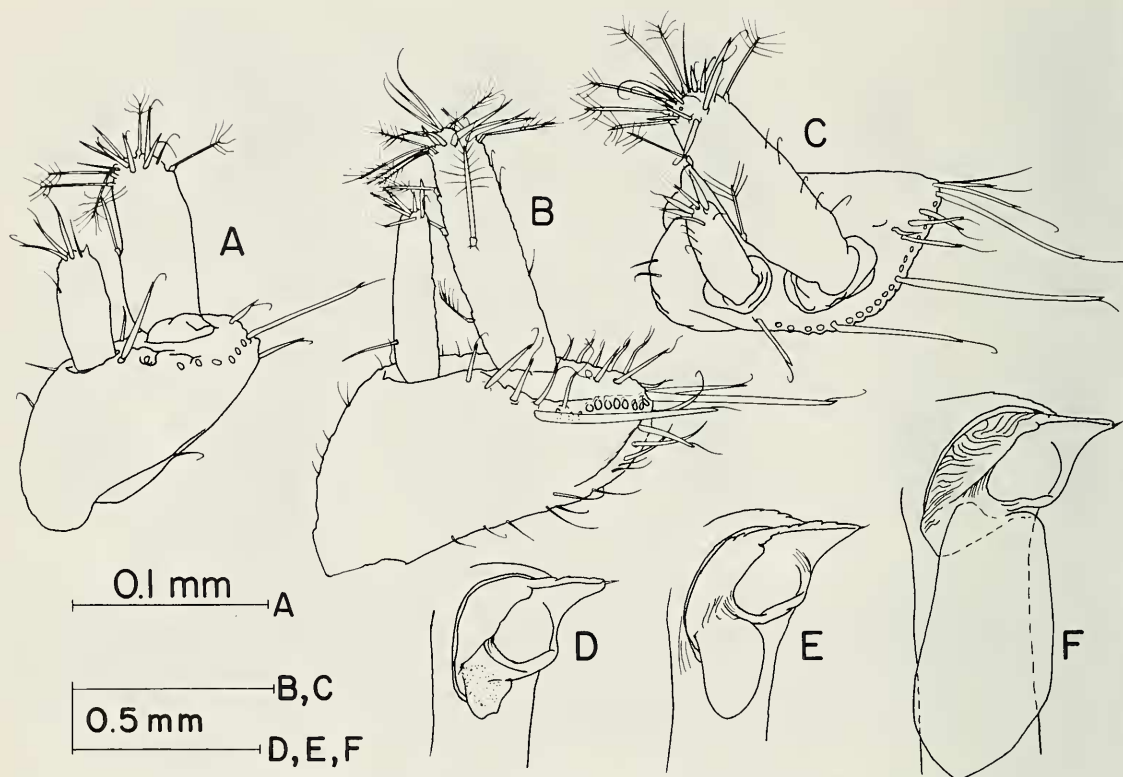
Fig. 9.   A–C, Uropoda: A, Stage 4 individual; B, Preparatory 2 female; C, Copulatory male, posterior view. D–F, Developing oostegites: D, Preparatory 1 female; E, Preparatory 2 female; F, Preparatory 3 female.

Rostrum.—In spite of the variability associated with the rostrum, there are some developmental components that can be recognized (Fig. 8). In mancas and stage 4, the rostrum is fairly broad: rostral-cephalic width ratio around 0.15. With maturity, the rostrum narrows to a ratio of around 0.10, although in some males this can be as small as 0.05. The rostral-frons over-hang can be seen to increase with age, ranging from 0.0 to 0.12 in the earliest stages to 0.10–0.33 at maturity. Mature males also tend to have greater overhang values than females. Between-individual variability in rostral shape also seems to increase with age such that all the manca and stage 4 individuals within a sample appear very similar while adults can be sub-stantially different.

Uropoda.—On the uropod (Fig. 9A–C), key taxonomic characters remain relatively unchanged through the life cycle: the endopod is always shorter than the width of the protopod, and the exopod length is always greater than half the endopod length. However, in the mancas the rami are thicker than in the adults: the endopod-protopod width ratio is 0.35; in mature adults this decreases to around 0.31 and 0.24 for males and females respectively. Note that the males retain some width; they also have endopods that are

slightly longer than females. The protopodal row of long, thin unequally bifid setae increases allometrically with size: in the manca 3, it has around 8–9 setae; in adults there are 20–22 setae, with no apparent dimorphism in this or other setal characters.

Oostegites and female maturation.—Four separate stages of development of the oostegites could be recognized in *Eurycope iphthima* (Fig. 9D–F). Wolff (1962) previously recognized a great variation in the sizes of developing oostegites in several eurycopids and munnopsids, but could not relate them to a developmental sequence for lack of data. The material of *E. iphthima* clearly shows that the increase in the size of the rudimentary oostegites is correlated with somatic growth and is a direct consequence of approaching maturation in females. The female juvenile phase, that is, individuals with no evidence of oostegite buds but not mancas, always spans stages 4 and 5, although it clearly goes into stages 6, 7 or larger in some individuals. Therefore one can find outwardly 'juvenile' females from 2.0 to an observed maximum of 5.6 mm. It is not known whether the large 'juveniles' represent totally non-reproductive individuals or females that have brooded once. These largest females are at least one stage larger than the smallest brooding females.

Preparatory 1 females are characterized by rudimentary oostegites which appear as small buds on the medial edge of the coxae of the first 4 pereopods (Fig. 9D). The tissue below these buds appears to be somewhat more dense and granular, thus aiding their identification. There was some interindividual variation in size of the buds but none approach the size of the next stage. Preparatory 1 females occurred at lengths from 3.5 mm (stage 6) up to 5.8 mm, well beyond stage 9.

A second rare state occurs where the rudimentary oostegite is approximately the same size as the coxa (Fig. 9E). Only one or two preparatory 2 females were found at each station, varying in length from 4.9 to 7.0 mm. The rarity of this state may be due to most females passing directly from preparatory 1 to preparatory 3 in one molt.

The preparatory 3 oostegite is much larger than the coxa but not extending to the midline (Fig. 9F). This condition was found in females as small as 4.6 mm (stage 8 or 9) to as large as 7.5 mm. The females in this state should be considered as being fully copulatory and sexually mature, because this is the final stage before brooding. In support of this assertion, Veuille (1978b) has shown that in *Jaera* the final preparatory females receive the males. Furthermore, several preparatory 3 females of *E. iphthima* which were dissected proved to have apparent cuticular organs and gonads full of oocyte material. In this state the oostegites were observed to vary from being thin, transparent lamellae to fat opaque pads. That these latter oostegites are in a premolt condition is shown by the presence of developing structures under the old cuticle.
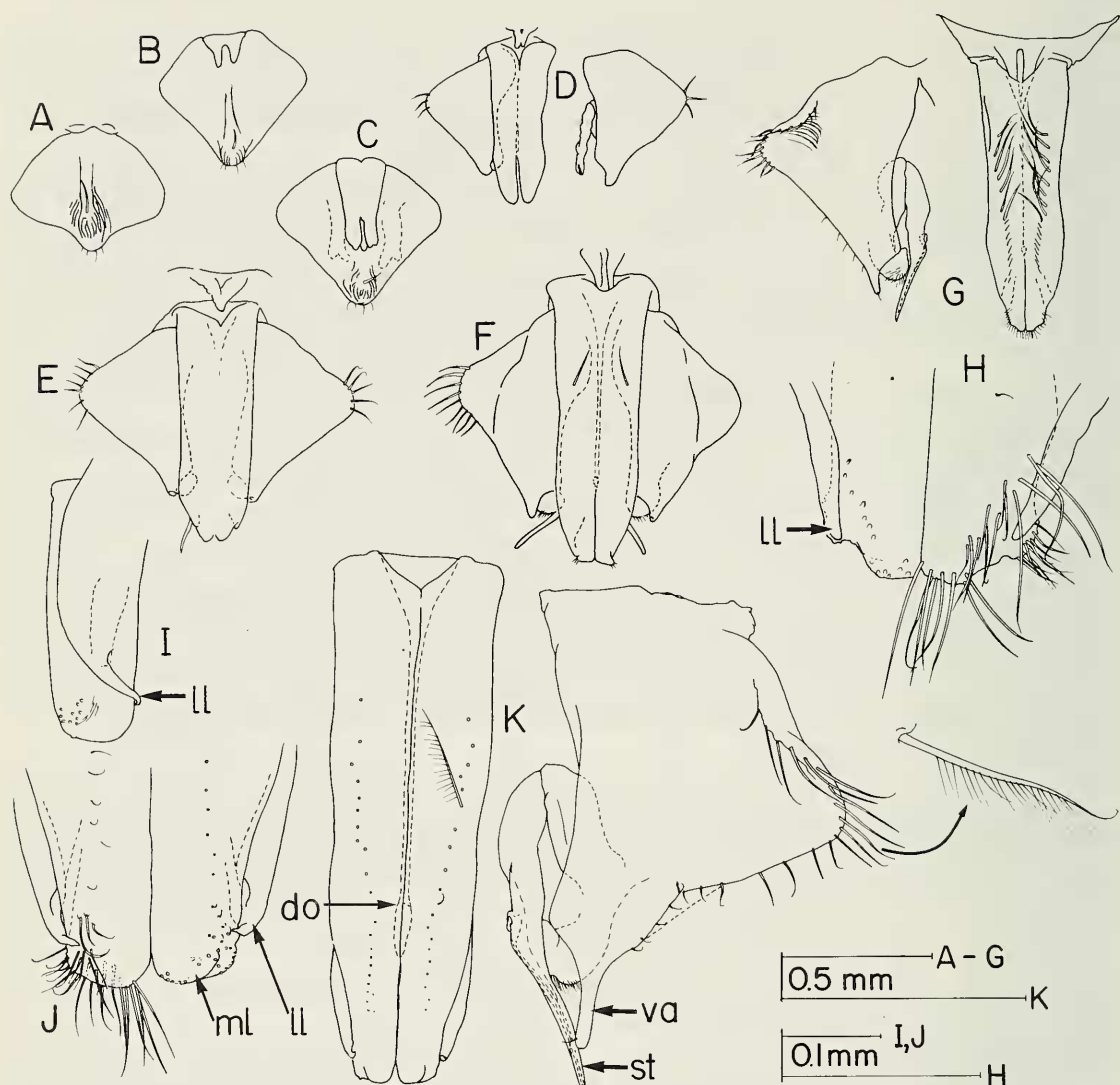
Fig. 10.   Development of male pleopods I and II. A–C, Stage 4 individuals, all 2.2 mm long; D, Stage 5, 2.6 mm; left pleopod II detached to show developing stylet; E, Stage 7, 3.7 mm; F, Juvenile stage, 4.6 mm; G–H, Precopulatory male 4.4 mm; G, Pleopods separated; H, Enlargement of pleopod I distal tip, spines on lateral lobes straight, setae omitted from left side; I–K, Copulatory male, 5.4 mm, setae if omitted shown by their insertions; I–J, Pleopod I distal tip, lateral (showing curved spine) and ventral views, *ml*—medial lobe, *ll*—lateral lobe; K, Ventral view, pleopods separated, enlargement shows hemiplumose seta typically found in rows on venter of pleopod I and lateral margin of pleopod II, *st*—stylet, *va*—vermiform appendage, *do*—proximal edge of dorsal orifice.

In the final brooding condition, the oostegites become quite large and form the typical isopodan brood chamber. The oostegal lamella is very thin with an axial thickening for stiffness, and with several groups of fine sensory setae on the external surface. Brooding females were fairly rare in the collections and ranged in size from 4.5 to 5.8 mm. Because preparatory 3 females longer than 7 mm were found, it is reasonable to suppose that the

brooding female can attain this size. The size-spread in mature and brooding females indicates that this species may reproduce at least twice in a life cycle. If this is the case for the eurycopid species examined by Wolff (1962), his data on oostegite and body size are easily explainable within the framework of the present study.

Male pleopods I and II.—Bocquet (1953) demonstrated that the male pleopod development in *Jaera* is not rigidly associated with particular instars. Similarly, these sexual characters of male *Eurycope iphthima* show considerable variation in their development. Two types of variation were recognized: the stage at which the pleopod begins to develop, and the degree of development of the pleopods at any one instar. Pleopod I appears in the manca 3, as in other deep-sea asellotes (Wolff, 1962; Hessler, 1970; Haugsness and Hessler, 1979), or later in stage 4 or 5. Males with developing pleopods were found over a broad range of sizes (2.0–4.9 mm). If the total variation in the development of pleopod I is considered, a gradual maturation is seen, although for each individual the pleopod growth is no doubt saltational. Consequently, it was not possible to classify the stages of male maturation other than to note when a male was fully copulatory.

At first appearance the first pleopod is a flat, bifurcate lobe of variable size above an undifferentiated pleopod II (Fig. 10A–C). In the degree of development shown in Fig. 10C the primordia of the endopod and exopod of pleopod II can be seen underneath the cuticle. As the instars proceed, the first pleopod extends to its full length relative to the pleotelson, and the second pleopod separates with the endopod and exopod becoming external, but undeveloped (Fig. 10D). Hemiplumose setae (Fig. 10K) appear in rows on the lateral margins of pleopod II and the ventral surface of pleopod I. The penile papillae enlarge and enter the anterior funnel of the first pleopods while the medial lobe separates from the lateral lobe and becomes more setose. At this point the stylet is fully elongated and its sperm duct is complete and open. During this development the distal tip of pleopod II becomes produced into a thin projection of variable length, the vermiform process, which in copulatory males (Fig. 10K) is nearly as long as the exopod. The pleopod I lateral lobe changes in the final molt from a straight spine (Fig. 10H) to a ventrally-curving spine (Fig. 10I).

Anomalous sexual development.—At WHOI 328 one 4.9 mm long individual was distinctly larger than stage 7, but had a developing male pleopod I on top of an undifferentiated female-like pleopod II. The second largest male (6.0 mm) at WHOI 326 was observed to have an antennula intermediate in development between mature males and females. Several of the largest males from these collections are only in the precopulatory stage, based on pleopod morphology, while smaller males are fully copulatory. Similar observations are found in other deep sea species. Hessler (1970) reports a very large preparatory male of *Chelator vulgaris* which exhibits feminine-like

features, and the large illustrated male of *Eurycope ratmanovi* Gurjanova (1946) has immature pleopods. These anomalies may well represent manifestations of protogynous hermaphroditism, wherein a female may go through one brooding cycle and then changes into a male. Both in *E. iphthima* and in *C. vulgaris,* the unusual males are the same size or larger than the smaller modes of brooding females. Protogynous hermaphroditism has been reported for other janiroideans (Wolff, 1962) and is indicated by adult intersex individuals of Haploniscidae, Ishnomesidae, Pleurogoniidae, and other Eurycopidae (unpublished data). These latter individuals had both developing male pleopods and female characters, either oostegites or cuticular marks of the egg-laying organ (see Veuille, 1978b). It is important to note that some past reports of intersexes in deep-sea isopods, i.e., *Haploniscus percavix* Menzies (1962), are probably juvenile developing males. In spite of this possible confusion, the hermaphroditic condition may be much more prevalent in deep-sea isopods than previously thought. This certainly has proved to be the case in tanaids of the family Neotanaidae (Gardiner, 1975).

Discussion.—Hessler (1970) notes the development of most desmosomatid species appears to be rigidly scheduled as in *Haploniscus biscuspis* Wolff (1962). The size-frequency data on *Bellibos buzwilsoni* Haugsness and Hessler (1979) also seems to agree with this. However, Thistle and Hessler (1977), reporting on *Betamorpha characta* Hessler and Thistle (1975), describe some variability in the form of the immature male pleopods I and II, and could not discern any development of these male pleopods in the manca 3 stage.

Somatic growth in *E. iphthima,* at least for the earliest stages, is rigidly determined; stage 4 individuals always fall within a few tenths of a millimeter of 2.2 mm, regardless of the locality. In contrast to this, the stages of sexual development for both males and females have broad size ranges over several localities, clearly spanning a number of instars. Because the observed range of instars for levels of reproductive development is more restricted within localities, one possible function of this flexibility may be to allow a deme of the widespread *E. iphthima* more readily to adapt to local environmental conditions.

The results on this species indicate that there are 2 components to development that need to be considered: somatic growth, described as the succession of instars; and sexual development, described as the appearance of primary and secondary sexual characters. In most desmosomatids, the appearance of sexual features is closely coupled with somatic growth, while in *E. iphthima* and in the genus *Jaera* there is some independence between these two components.

However, observed variation of sexual development may require consideration of two different phenomena, decoupled sexual development, and

hermaphroditism. Thus, *Chelator vulgaris* is an example of rigidly coupled sexual and somatic development with protogyny, *Jaera* shows some decoupling of sexual growth, and *Eurycope iphthima* displays characteristics of both influences on development.

Acknowledgments

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